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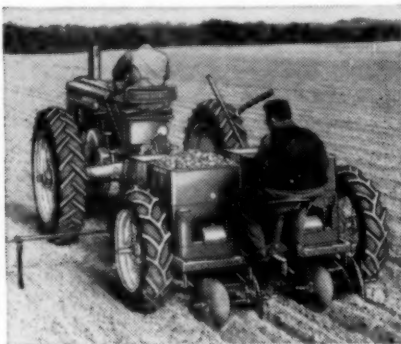
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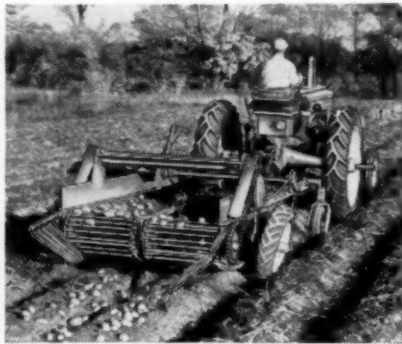
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*Data presented by J. W. Heuberger, Delaware Agr. Expt. Sta. at 1951 meeting of Potato Assoc. of America, Cincinnati, Ohio.

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CHEROKEE:¹ A NEW MEDIUM-MATURING POTATO
VARIETY RESISTANT TO COMMON SCAB, LATE BLIGHT,
MILD MOSAIC, AND NET NECROSIS

C. E. PETERSON,² N. K. ELLIS,³ R. V. AKELEY,⁴ AND F. J. STEVENSON⁴

Common scab is becoming a limiting factor in potato production in some of the best potato-producing areas of the United States, especially in the rich muck soils of the north-central region. The organism inciting this disease (*Streptomyces scabies* (Thaxt.) Waks. & Henrici) is carried on seed potatoes and also lives over from year to year in the soil.

In the past, control of common scab has been attempted by seed treatments and to a limited extent by crop rotations and soil treatments. A number of seed treatments for killing the common scab organism on the seed potatoes have been recommended; although such treatments are effective in reducing or preventing the introduction of the organism into clean soil, scab has become so widely prevalent in many commercial potato areas that seed treatment for control of this disease seems of little or no value.

Potatoes grown in highly acid soil (pH 5.2 or below) are rarely scabby, but it is often difficult to maintain the proper acidity, especially where it is desirable to supply lime for leguminous crops in the rotation, such as alfalfa or clover.

The amount of scab found on a potato crop is dependent not only upon the soil but also on climatic conditions and physiologic races of the causal organism. As a result, the intensity of scab epidemics varies from year to year and from place to place. In certain potato-growing sections scab epidemics are becoming more severe in spite of seed treatments, soil treatments, and recommended cultural practices; so there is an increasing demand from growers for scab-resistant varieties. Two of the old varieties, Russet Rural and Russet Burbank, and a sport of Sebago called Russet Sebago seem to have some resistance to scab. This resistance is more apparent than real since the number of infections may be as great on the russet-type as on the smooth-type, but the lesions are usually less conspicuous. However, under very favorable conditions for the production of scab the lesions on the russet-type become so enlarged that many of the tubers are not marketable as U. S. No. 1's. This situation

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¹Cherokee, an Indian of an Iroquoian tribe, now chiefly in Oklahoma.

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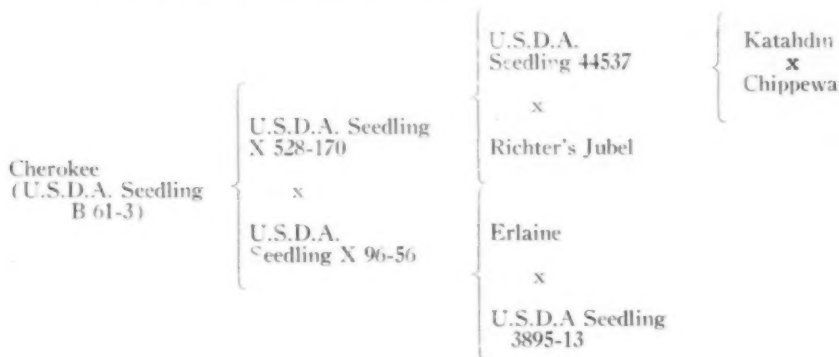
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occurred in the scab test at Shafter, California, in 1952. Only 6 per cent of the tubers of Russet Burbank were marketable. In contrast, a number of scab-resistant seedling varieties in the same test produced 100 per cent marketable tubers.

Most of the old American varieties such as Irish' Cobbler and Green Mountain are very susceptible to scab. A few European varieties such as Hindenburg, Jubel, Ostragis, Rheingold, Arnica, and Ackersegen vary somewhat in reaction to scab, but all are more resistant than any of the old American varieties. None of the European sorts is immune nor has any commercial promise in the United States but when they were used as parents in crosses with domestic types many scab-resistant varieties were produced. Five of these, Cherokee, Menominee, Ontario, Seneca, and Cayuga have been released to growers. Cherokee has the advantage over the other four in two respects: it is medium early and highly resistant to the common races of the late blight fungus.

The pedigree of Cherokee follows:



DESCRIPTION

Plants. Medium sized, spreading; stems thin, prominently angled; nodes slightly swollen, slightly pigmented, reddish purple; wings prominent, slightly waved, slightly pigmented; stipules medium large, green, scantily pubescent; leaves medium sized to large, midribs slightly pigmented, scantily pubescent; petioles slightly pigmented, scantily pubescent; terminal leaflets large, broadly ovate, acuminate, asymmetrical; primary leaflets 3 pairs, large, elliptical-ovate, mean length of blade 68.4 ± 0.6 mm. (2.7 in.), mean width 44.6 ± 0.5 mm. (1.8 in.), index 65.2 ± 0.5^5 ; leaflet petioles slightly pigmented; secondary leaflets few, between pairs of primary leaflets; tertiary leaflets few; inflorescence medium branched, bracts medium in number, peduncles on main stem and in axils of petioles, medium in length, slightly pigmented, scantily pubescent; pedicels short, slightly pigmented, scantily pubescent.

⁵Calculated by dividing the width of each 100 leaflets by their length and multiplying the average of these ratios by 100. The leaflets were taken from the fourth leaf from the top of the stem, one leaflet, the distal left lateral, being taken from each leaf. Since the potato leaflet is asymmetrical the length was determined by taking the average of the measurements from the apex to the base of each respective lobe. This is a modification of the method described on pages 163 to 170 of Salaman, R. N., *Potato Varieties*, (378 Pp.) Cambridge 1926.

Flowers. Calyx lobes short (4-6 mm.), awl-shaped; calyx tips straight, green, scantily pubescent; corolla medium in size (25-31 mm.), white; anthers orange yellow; pollen medium abundant, of good quality; styles straight; stigma globose, multilobed, green.

Tubers. Predominately short elliptical, somewhat flattened, frequently having a distinct flattened area on one side toward the stem end. Mean length 86.1 ± 0.5 mm. (3.4 in.)⁶, mean width 77.8 ± 0.5 mm. (3.1 in.)⁶, mean thickness 56.8 ± 0.5 mm. (2.2 in.)⁶, indexes, width to length 90.6 ± 0.8^7 , thickness to length 66.2 ± 0.9^8 , thickness to width 73.1 ± 0.8^8 . Skin slightly flaked, self-colored, ivory yellow (considered white in the commercial trade). Eyes medium shallow, of same color as skin. Flesh white. Maturity medium early.

CHARACTERISTICS

Cherokee is medium early in maturity. It was tested for 4 years on muck soil at Clear Lake, Iowa. Some of the soil in this section has become so heavily infested with the common scab organism that susceptible varieties such as the Irish Cobbler can no longer be grown profitably. Cherokee has shown a high degree of resistance to scab in this area. It is resistant also to mild mosaic and net necrosis. At the present time it has not contracted mild mosaic in the field-exposure tests in Maine. However, when exposed to leaf roll in the field in Maine it has shown a small percentage of net necrosis. In these tests the 2-year average (1950-51) was 5.2 per cent net necrosis for Cherokee as compared with 41.0 per cent for Green Mountain.

In the 4 years of tests at Clear Lake, Iowa, Cherokee produced an average of 561 bushels of U. S. No. 1 potatoes per acre as compared with 467 bushels for Irish Cobbler and 542 bushels for Sebago as revealed in table 1.

TABLE 1.—*Yields per acre of U. S. No. 1 potatoes and percentage total solids in Cherokee, Irish Cobbler, and Sebago tested on muck soil for 4 years at Clear Lake, Iowa, 1948-1952.*

Year Tested	Cherokee		Irish Cobbler		Sebago	
	Yield per Acre	Total Solids ¹	Yield per Acre	Total Solids ¹	Yield per Acre	Total Solids ¹
	Bus.	Per cent	Bus.	Per cent	Bus.	Per cent
1948	547	19.2	481	17.9	374	17.4
1949	447	18.2	486	16.5	511	17.4
1950	704	18.6	415	17.3	501	18.6
1952	547	19.0	487	18.6	782	18.7
Mean	561	18.8	467	17.6	542	18.0

¹Based on specific gravity of the tubers.

⁶Average measurements of 64 tubers each of a weight of approximately 8 ounces.

⁷Calculated by dividing the width of each of 64 tubers by their length and multiplying the average of these ratios by 100. The data used for calculating the indexes were taken from the measurements used to designate the dimensions of the tubers.

⁸Based on the measurements of the tubers used for determining the width to length index and calculated by the same method.

In 1950 in Indiana the average yield of Cherokee in four locations on muck soil was 30 per cent higher than that of Irish Cobbler but 5 per cent lower than that of Katahdin. In 1951 Cherokee outyielded Irish Cobbler by 44 per cent but yielded about $3\frac{1}{2}$ per cent lower than Katahdin.

In Maine in tests conducted cooperatively by the United States Department of Agriculture and the Maine Agricultural Experiment Station the 5-year average yield for Cherokee was 526 bushels per acre as compared with 476 bushels for Irish Cobbler and 487 bushels for Katahdin, which you will note in table 2.

TABLE 2.—Total yields per acre and percentage total solids in Cherokee, Irish Cobbler, and Katahdin grown in a number of locations in Maine for 5 years, 1947-1952.

Year Tested	Locations	Cherokee		Irish Cobbler		Katahdin	
		Mean Yield per Acre	Total Solids ¹	Mean Yield per Acre	Total Solids ¹	Mean Yield per Acre	Total Solids ¹
	No.	Bus.	Per cent	Bus.	Per cent	Bus.	Per cent
1947	4	569	19.9	539	19.4	521	18.1
1948	6	515	20.4	468	19.9	470	19.1
1950	6	626	17.9	553	17.9	571	17.3
1951	4	527	17.9	439	17.9	489	17.9
1952	4	347	18.6	345	18.9	351	17.1
Mean of 24 tests		526	19.0	476	18.8	487	18.0

Cherokee has been promising in yield trials in other states. Dr. O. C. Turnquist, University of Minnesota, University Farm, St. Paul, Minn., tested it for 3 years (1950-1952) in various locations in Minnesota in comparison with a number of named and numbered varieties. The data for total yield for these tests are given in table 3. Cherokee outyielded the standard variety Irish Cobbler in 9 out of 11 tests and Katahdin in 6 of 7 tests.

The tubers of Cherokee have an attractive ivory yellow skin. The tuber is predominantly short, elliptical, and somewhat flattened, and frequently a tuber has a distinct flattened area on one side toward the stem end. In Minnesota the tubers are often slightly concave on the dorsal side. Under adverse conditions Cherokee tubers are inclined to be more irregular than those of Katahdin. Notwithstanding the fact that Cherokee has shown a tendency to produce irregular shapes and second growth in a few locations, its tubers when grown in muck soil in Iowa and Indiana have not been so rough as those of Irish Cobbler. Because of the smoother skin and the absence of common scab, the tubers of Cherokee are much more attractive than those of Irish Cobbler. Growers of this variety in Indiana are advised to watch its progress closely as it approaches maturity, so that if knobs begin to form on the tubers, the vines may be killed immediately to stop growth. Such killing reduces the total yield, but the percentage of U. S. No. 1 potatoes is greater.

TABLE 3.—*Total yields per acre of Cherokee, Irish Cobbler and Katahdin in several locations in Minnesota, 1950-1952.*¹

Year	Location	Type of Soil	Yield per Acre		
			Cherokee	Irish Cobbler	Katahdin
			Bus.	Bus.	Bus.
1950	St. Louis County	Upland	474	397	457
1950	Freeborn County	Muck	791	622	863
Mean			633	510	660
1951	Baker	Red River Valley	256	250	194
1951	Fisher	"	355	273	142
1951	Stephen	"	355	302	158
1951	Donaldson	"	361	256	140
1951	Brooklyn Center	Sandland	314	—	241
Mean			328	270	175
1952	Hollandale	Muck	534	551	—
1952	Baker	Red River Valley	224	248	—
1952	Fisher	"	302	281	—
1952	Donaldson	"	301	269	—
1952	Brooklyn Center	Sandland	454	394	—
Mean			363	349	—

¹Data of O. C. Turnquist, University of Minnesota, University Farm, St. Paul, Minn.

In 1950 O. C. Turnquist reported from Minnesota as follows:

Included in the tests was a numbered selection, B 61-3 (Cherokee), a mid-season variety with a combination of scab and late blight resistance. The tubers appeared to be round to oval and flat to fairly plump. On some occasions in the past this variety has been inclined to become rough but this characteristic was not too apparent in the tests this year. The tubers have a paper-white skin with the appearance of an artificially waxed potato. It (B 61-3) appears to resist bruising and abrasion and holds up well in storage. No scab or late blight infection was observed on tubers of B 61-3.

The tubers of Cherokee store well in Maine. However, in 1951 in Indiana they (the tubers of Cherokee) seemed to become especially sweet in storage. This condition was not reported for any of the tests in other states.

In Iowa the percentage of total solids in the tubers of Cherokee for four years was as high as or higher than that found in the tubers of Irish Cobbler; these findings would indicate satisfactory quality for that state. (See table 1).

In Maine the cooking quality of Cherokee has been graded medium to high. The total solids found in Cherokee (average of 24 tests) was 19 per cent as compared with 18.8 per cent for Irish Cobbler and 18 per cent for Katahdin as you will observe in table 2. The differences were

probably not significant, but the data do indicate that the Cherokee is usually as high as or higher in percentage of total solids than Irish Cobbler or Katahdin.

Cherokee is the first variety to be released under the National Potato Breeding Program that is highly resistant to common scab, highly resistant to the common races of late blight, apparently field immune from mild mosaic, and somewhat resistant to net necrosis.

SUMMARY

Cherokee (B 61-3) is resistant to common scab, late blight, mild mosaic, and net necrosis. In comparative trials in Iowa, Indiana, Minnesota, and Maine it has outyielded Irish Cobbler in nearly all tests, and on the average its tubers have been higher in total solids than those of the Irish Cobbler. It should be a very valuable variety for growers who have soil infested with scab organisms or who have difficulty in controlling late blight.

PERIDERM DEVELOPMENT OF THE POTATO TUBER AND ITS RELATIONSHIP TO SCAB RESISTANCE¹

D. C. COOPER², G. W. STOKES³, AND G. H. RIEMAN⁴

Potato varieties differ in their reaction to *Streptomyces scabies*, the organism which causes the disease designated as common scab. A large number of the commercial varieties are highly susceptible to this pathogen. When they are grown in plots where the fungus is present in the soil they will produce tubers that are more or less covered with scab lesions if conditions are favorable for infection during the period of tuberization. The commonly grown varieties, Irish Cobbler, Triumph, Katahdin, Chippewa, and Pontiac, fall into this category.

A limited number of varieties, *e. g.* Ontario, Menominee, Cherokee and Hindenburg are noted for their clean tubers even though the plants are growing under conditions favorable for the disease. Some varieties which produce tubers with a russet skin, *e. g.* Russet Rural and Russet Burbank are classified as tolerant. This is probably a result of the fact that the lesions are frequently relatively small and inconspicuous. When such varieties are grown under conditions exceptionally favorable for infection the lesions become more prominent. No known potato varieties are immune to scab.

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³Assistant Plant Pathologist, University of Kentucky.

⁴Professor of Genetics, Plant Pathology and Horticulture, University of Wisconsin.

Several suggestions have been advanced to offer an explanation for the nature of the resistance exhibited by some varieties. Lutman (5) concluded that it is the thickness of the skin of the tuber which determines its resistance to scab and that color plays little, if any, role. Since tubers of Russet varieties have thicker skins than do those of smooth varieties, they were considered to be more or less resistant. Longree (4) could find no correlation between the final thickness of the tuber's skin and its resistance to scab. She decided that the lenticel is the region of entrance of the pathogen and that resistance is associated with a close packing of the "stuffing" cells in that corky area, the degree of corking and the limited ability to form wound periderm.

Darling (1) found that some of the most resistant seedlings used in his tests produced tubers with smooth skins which indicated that scab resistance is not necessarily associated with a russet skin. It was his conclusion that the lenticel is the chief avenue of infection. When the size and the structure of the lenticels on tubers of susceptible and resistant lines were compared he found that those of the former are large and composed of loosely arranged, spherical cells whereas those of the latter are smaller and consist of small, closely associated, suberized cells. Thus the lenticel of the susceptible type furnishes a suitable infection court whereas that of the resistant type presents a barrier to the pathogen.

Fellows (2) concluded that the tuber must be actively growing if infection is to take place. Wingerberg (12) decided that resistance rests on a physiological basis but did not offer an explanation for the nature of such reaction. Johnson and Schaal (3) noted a close correlation between the amount of chlorogenic acid in the peripheral layers of the tuber and resistance to scab. Varieties differ in the amount of this acid present in the cortical region of the tuber. Those having a relatively high amount of chlorogenic acid proved to be notably resistant. Susceptibility increases as the quantity of such acid decreases. A susceptible variety possesses approximately half as much chlorogenic acid per given sized sample as does the resistant variety. They offer two suggestions as to the effect of chlorogenic acid, either (1) it lowers the pH of the cells thereby creating an unfavorable medium for the growth of the fungus or (2) the acid itself or its quinone may be directly or indirectly involved in the formation of the suberized periderm.

OBSERVATIONS

The course of development of the periderm during the early stages of tuberization and its nature at tuber maturity have been determined for five named varieties of potatoes and a number of seedlings. The epidermis of the tuber primordium is ephemeral and disintegrates shortly after enlargement is initiated. An epidermis is regularly becoming differentiated near the apex of the growing tuber. It persists for a brief period and then breaks down. The hypodermal layer, as indicated by Reed (6), functions as a phellogen and by periclinal and anticlinal cell divisions produces a periderm which ranges from five to eight layers of cells in thickness. The inner layers of the periderm remain meristematic throughout the growth of the tuber and produce new phellem cells. Simultaneously the cortical layers become disorganized so that the thickness of the functional periderm remains uniform during the course of tuber enlargement.

The outermost layers of periderm cells of the tubers of some varieties, *e. g.* Ontario and Hindenburg, are disintegrating and being shed continuously during the course of tuber enlargement so that the periderm is, as a rule, composed of living, nucleated cells. The number of layers of cells in such periderms remains relatively constant throughout the course of tuber development.

The cells of the external layers gradually become senescent, die and collapse forming a mantle of defunct tissue on the surface of the tubers of other varieties such as Irish Cobbler, Triumph and Katahdin. The nuclei of the aging cells shrink in size and ultimately disintegrate prior to the collapse of the cells. This extraneous material cracks and breaks as the tuber enlarges so that irregularly shaped masses of dead cells adhere to the surface of the tuber. Such masses range from a few to 20 or more cell layers in thickness.

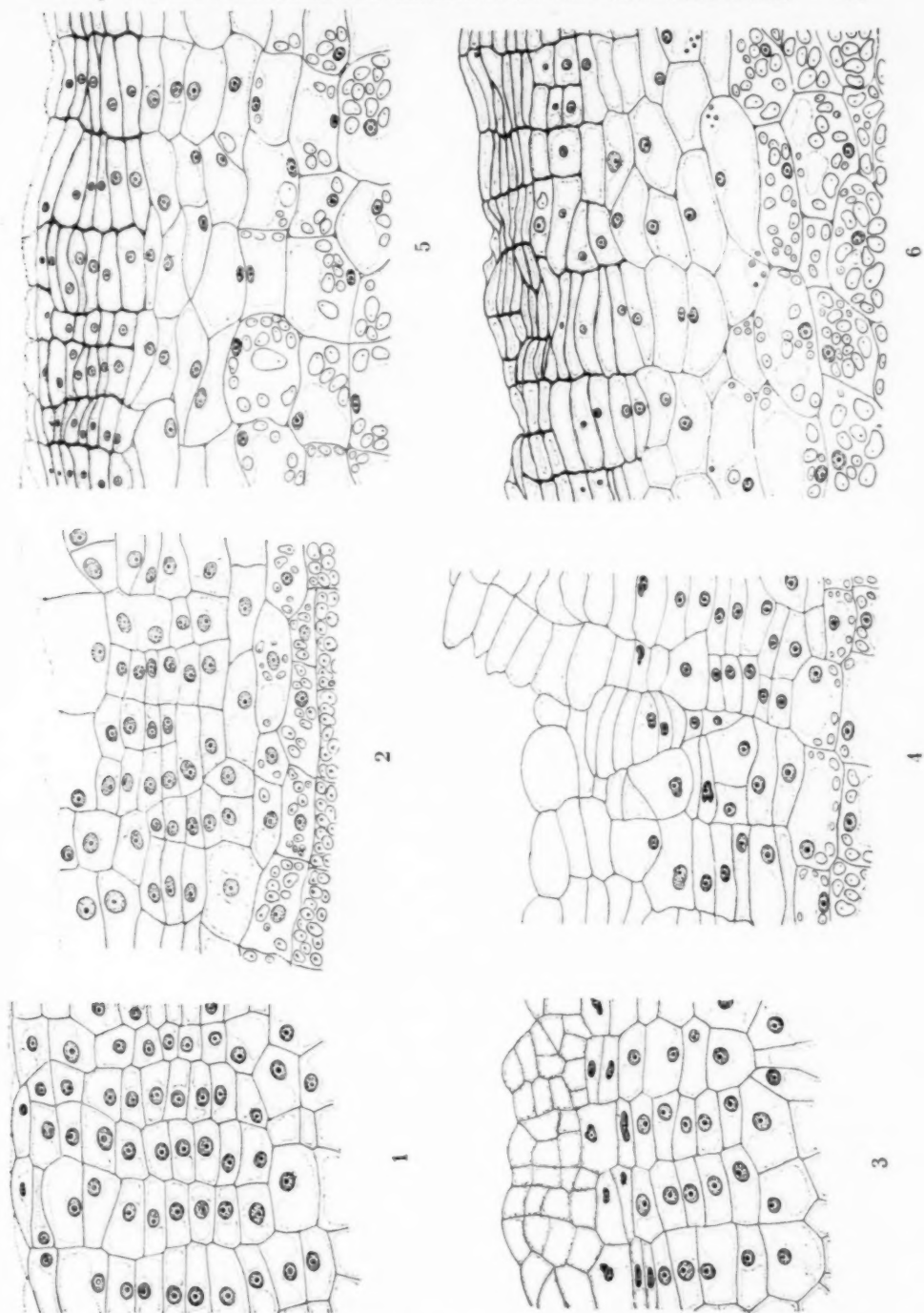
There appears to be a close correlation between the presence of layers of collapsed cells on the surface of the developing tuber and its susceptibility to common scab. Those varieties which have a considerable amount of defunct tissue adhering to the surface of the growing tuber are prone to produce "scabby" potatoes if the causative organism is present in the soil and climatic conditions are favorable for infection. The two varieties where the peripheral layer of the tuber is regularly disintegrating and being sloughed off so that the periderm, for the most part, consists of living, nucleated cells are highly resistant to the scab-producing organism.

When it was realized that such a distinct histological difference existed, developing tubers of a number of varieties were examined to determine the nature of the periderm during the course of tuber enlargement. Tubers ranging from five to 50 mm in diameter were collected and examined.¹ Particular attention was given to the younger tubers since Sanford (7,8) has shown that scab infection occurs during the early stages of tuberization.

The periderms near the basal ends of 5 mm and 10 mm tubers from the resistant varieties, Cherokee and Iowa 6316 respectively, consist of nucleated cells that form a living tissue as shown in figures 1 and 2. Only the outer layers show evidences of disintegration. The periderms range from six to eight layers of cells in thickness.

The peripheral layers of cells from similar sized tubers of the susceptible varieties, White Cloud and Chisago, are composed of enucleated cells. Three or four layers on the surface of a 5 mm tuber lack nuclei as you will note in figure 3. The number of such layers has increased by the time the tuber has become 10 mm in diameter as you will see in figure 4. There are evidences of nuclear breakdown in the cells immediately below the peripheral layers of enucleated cells.

¹Satisfactory preparations for microscopic examination of the periderm of the potato tuber may be prepared as follows:— (1) Make a thin, free-hand section through the desired portion at a right angle to the surface of the tuber, (2) Place the section in a drop of aceto-carmin on a clean slide, (3) Put a cover glass in place taking care not to crush the section, and (4) Gently warm the slide over an alcohol flame but do not bring to the boiling point. The preparation is now ready for examination.



FIGURES 1, 2, and 5. Periderms of tubers of the scab resistant varieties, Cherokee (5 mm tuber), Iowa 3616 (10 mm tuber) and Hindenburg (25 mm tuber), respectively.

FIGURES 3, 4, and 6. Periderms of tubers of the scab susceptible varieties, White Cloud (5 mm tuber), Chisago (10 mm tuber) and Triumph (25 mm tuber), respectively.

The cell walls of the periderms from tubers of both resistant and susceptible varieties ranging from 5 mm to 10 mm in diameter show little, if any, evidences of suberization. The anticlinal, and to a lesser extent the periclinal walls of the phellem cells become increasingly suberized during the further course of tuber development. In spite of this fact the outermost periderm layers of the tubers of resistant varieties continue, one after another, to disintegrate and the periderm persists as a living tissue. Little, if any, residue of the disintegrating cells remains on the surface of the tuber.

The outermost layers of enucleated cells on the tubers of susceptible varieties do not immediately disintegrate. As the tubers enlarge they collapse and form a defunct tissue which remains adherent to the surfaces of tubers. This difference is readily discernible when one compares the periderms of 25 mm (Figures 5 and 6) and 50 mm (Figures 7 and 8) tubers from the resistant Hindenburg and the susceptible Triumph varieties.

Since it has been assumed that the lenticel forms the natural avenue of entrance of the scab-inducing organism, a comparison of the structure of the lenticels as they occur on tubers of resistant and susceptible varieties was made to determine if there are any characteristic structural differences. All of the cells of the basal lenticels on 25 mm tubers of resistant varieties possess nuclei (Figure 9) and there are no evidences of cellular breakdown. Those of the peripheral layers usually contain some starch. The cells of the outermost layers of the lenticels on tubers of susceptible varieties are still plump but lack nuclei (Figure 10). They may contain an appreciable amount of starch and there are evidences of extraneous inclusions of one type or another.

The scab-inducing organism undoubtedly enters the senescent cells at the surface of the tuber prior to their collapse and penetrates the deeper layers of cells as they approach senescence. The defunct tissue on the surface of the tuber at later stages of development forms a satisfactory medium for the growth of an unrelated fungus. A septate mycelium is frequently found growing on the surface of tubers of susceptible varieties (Figure 11). This fungus is not to be confused with *S. scabies* since the diameter of the mycelium is eight to ten times that of the latter. No such fungus has, thus far, been found on the surface of tubers of resistant varieties where the outermost layer regularly disintegrates and the cells of the periderm are in a living condition.

A number of potato varieties have been examined in order to determine (1) whether one of the two types of periderm development of the tuber is regularly associated with resistance or susceptibility and (2) whether periderm readings might be taken as diagnostic evidence for the probable reaction between the variety and the pathogen. Plants of 7 resistant and 10 susceptible selections were grown in the greenhouse, each plant being given a code number. Their reaction to scab was already known since they had been grown for several seasons in plots where the soil is heavily infested with the causal organism in order to determine such reaction. The tubers were harvested and examined when they had reached a stage of development where they ranged from one to three centimeters in diameter. The outermost layers of the periderm of the tubers from ten of the plants consisted of a mantle of enucleated and more-

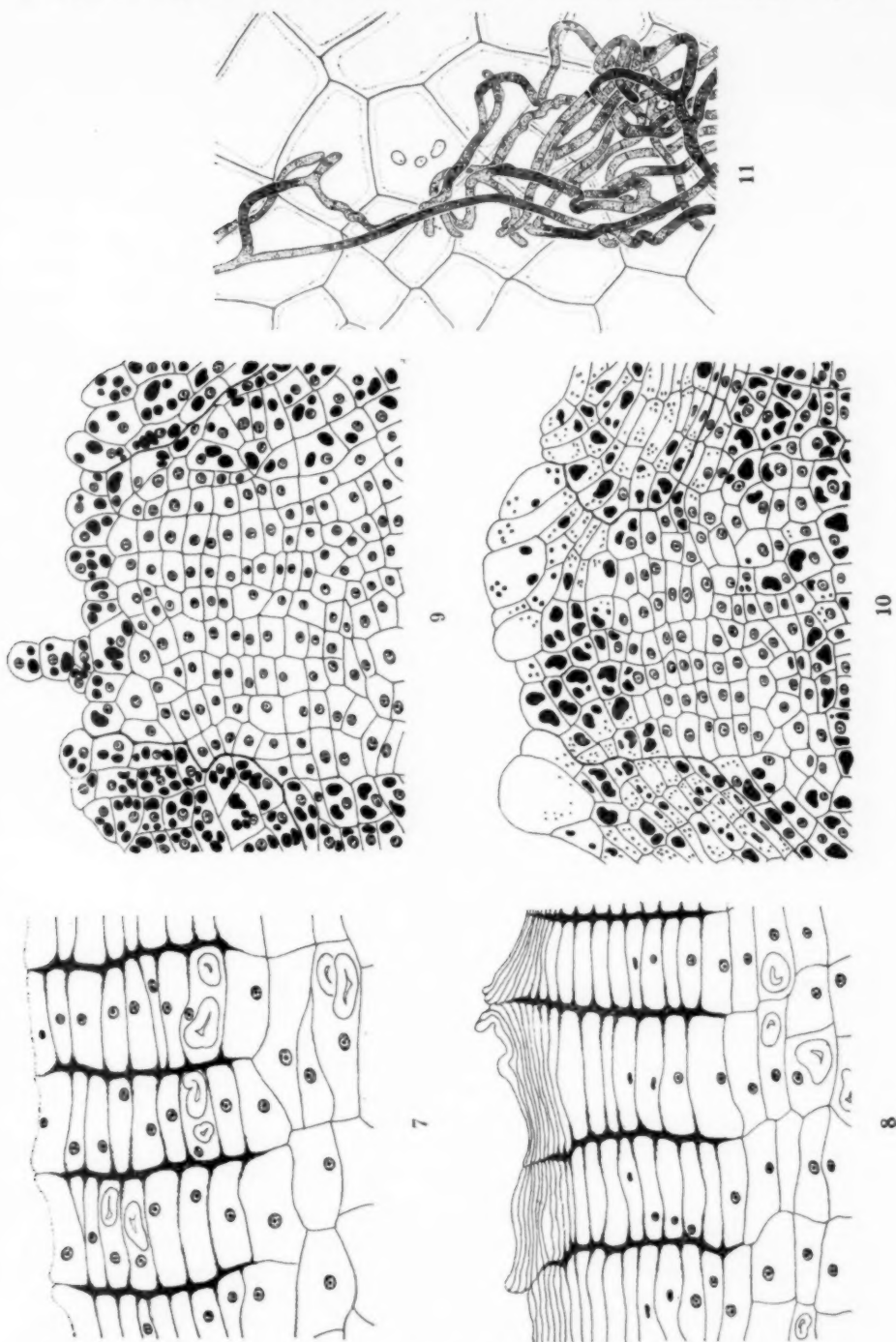


FIGURE 7. Periderm of a 50 mm tuber of the scab resistant variety, Hindenburg.
 FIGURE 8. Periderm of a 50 mm tuber of the scab susceptible variety, Triumph.
 FIGURE 9. L.S. of a lenticel from a 25 mm tuber of the scab resistant variety, M330.
 FIGURE 10. L.S. of a lenticel from a 25 mm tuber of the scab susceptible variety, Red Pontiac.
 FIGURE 11. Fungus occurring on the surface of a 25 mm tuber of a variety susceptible to scab.

or-less collapsed cells indicating that these plants were probably the susceptible selections. The entire periderm of the tubers from the remaining plants consisted of nucleated cells suggesting resistance. When these readings were checked against the planting data there was agreement in every instance (Table 1).

Young tubers were then collected from some of the lines being grown in the scab nursery at Antigo, Wisconsin. Each line had been assigned a field number. Periderm readings of tubers taken from seven of the lines disclosed several layers of collapsed cells adhering to the surface whereas no such covering was present on tubers from the remaining selections. When a comparison was later made with the planting data it was again found that the nature of the periderm proved to be an indicator of the probable reaction of the particular line to the pathogen. This comparison is clearly shown in table 2.

TABLE 1.—*Correlation of periderm reading of greenhouse material with scab reading in the field.*

Code No.	Periderm Reading	Variety	Scab Reading
1	L	M330	R
2	L	Ontario	R
3	C	Chisago	S
4	C	K5	S
5	L	Cherokee	R
6	C	Cobbler	S
7	L	Hindenburg	R
8	C	Satapa	S
9	C	Waseca	S
10	L	M439	R
11	C	Katahdin	S
12	C	Kennebec	S
13	C	White Cloud	S
14	C	Neb. 213.43-2	S
15	L	Iowa 6316	R
16	C	Triumph	S
17	L	B515-2	R

L = Periderm consists of living, nucleated cells.

C = Outer periderm consists of collapsed enucleated cells.

R = Resistant.

S = Susceptible.

DISCUSSION

Resistance to scab is apparently closely associated with the nature of the development of the periderm during tuberization. Varieties and seedling selections where the periderm persists as a living tissue throughout the period of tuber development are resistant to the scab-producing organism. Susceptibility to the pathogen occurs in those lines where a mantle of collapsed, defunct cells covers the periderm of the enlarging tuber.

Lutman (5) failed to call attention to these well-defined differences in periderm structure. He did present photomicrographs of transverse sections of the skins from a number of varieties of potatoes including both

TABLE 2.—*Correlation of periderm reading with field reading of plants growing in the scab nursery at Antigo, Wisconsin.*

Field No.	Periderm Reading	Variety	Scab Reading
A3	C	A3	S
A17	L	A17	R
V3	C	Waseca	S
V4	C	Satapa	S
V6	L	M804	R
V7	L	M439	R
V9	L	M304	R
V10	L	Minn. 113	R
V11	L	B515-2	R
V15	L	Iowa 6316	R
V18	L	Cherokee	R
V20	L	Ontario	R
V21	C	Chisago	S
V22	C	La Soda	S
V23	L	303-40	R
C	C	Chippewa	S
H	L	Hindenburg	R
RP	C	Red Pontiac	S

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resistant and susceptible lines. It is clearly evident from the series taken from developing tubers of the variety "Scab Proof" that the cells of the outer-most layers remain in a living, nucleated condition. This variety rates high in its resistance to scab. The peripheral layers of the tubers of susceptible varieties are composed of defunct cells. This is clearly evident when one compares Lutman's illustrations of the skins from resistant and susceptible varieties.

Darling (1) associated resistance with the time of suberization of the periderm. He found that the periderm becomes suberized while the tuber from a resistant seedling is quite small whereas there is little evidence of periderm suberization in tubers of comparable size from a susceptible seedling. Because suberization occurs earlier and extends further into the lenticels of tubers from resistant seedlings he concluded that this would afford a greater protection against infection. Since there is little, if any, evidence of suberization in the periderms of 10 mm tubers from either the susceptible "Chisago" or the resistant "Iowa 3616" lines it would appear as though resistance may not be closely associated with either the earliness or the amount of suberization.

It is common knowledge that resistant varieties, when grown on some types of soil or under certain climatic conditions may produce "scabby" potatoes. The lesions are seldom formed in the profusion that occurs on tubers of susceptible varieties and are usually of a superficial nature. In the light of the present findings this may be due to an unbalanced type of tuber growth under such conditions. The outermost layer(s) may not readily disintegrate and slough off. As a result a few layers of senescent cells might collect on the tuber's surface. Such layers

would probably persist for a time and then disintegrate following a return to normal growing conditions. If infection had taken place during this interim a lesion or lesions could have formed. Such a lesion would remain as a superficial structure following the decomposition of the unnatural accumulation of defunct tissue.

Numerous races of the scab-producing organisms have been isolated and described (Schaal, 9; Taylor and Decker, 10; Thomas, 11). Such races have been found to differ in morphology, physiology and pathogenicity. There is the possibility that certain of the more virulent strains may be able to enter into an interaction with the living cells of the periderm of the resistant varieties. This would explain the presence of the occasional lesion occurring on tubers of such lines.

One of the factors that is, at present, restraining the production and development of scab resistant varieties is the lack of a reliable diagnostic test for resistance at the seedling level. The more desirable selections must be propagated in a scab nursery for a number of years in order to ascertain their reaction to the pathogen. Determination of the nature of the periderm may prove to be of value in making scab resistant selections from seedlings or first generation clones that have other desired characters. The technique is quite simple and with a little practice one should be able to make a number of accurate readings, perhaps 40 or 50, within the course of a few hours.

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POTATO VIRUS A¹D. S. MACLACHLAN², R. H. LARSON³ AND J. C. WALKER³

Virus A is one of several viruses which incite mosaic diseases in the cultivated potato, *Solanum tuberosum* L. In susceptible varieties, virus A alone incites only a very mild mottle or is carried without production of symptoms. However, in combination with the milder mottle strains of virus X, it incites a moderate to severe mosaic disease, which in the older literature (2, 7, 13, 14, 15, 16) has been called potato crinkle, crinkle A, crinkle mosaic, as shown in figure 1A, veinal mosaic, and mild mosaic (Fig. 1B). Mosaic symptoms vary considerably depending upon the environmental conditions under which they are observed, the variety of potato infected, and the strains of the viruses involved. The names crinkle, and paracrinkle (16) may also be confused, but there is no demonstrated relationship between the viruses inciting these two diseases.

Identification of potato virus diseases in the field by the symptoms they incite on potato varieties has been a common practice. Recently (5, 10) it was demonstrated that there is a definite similarity of primary, as well as secondary symptoms caused by strains of potato virus X and virus Y, to those caused by other viruses. This also holds true with potato virus A. Green Mountain and Triumph potato plants infected with virus A exhibited symptoms indistinguishable from those of early infection with virus Y or with virulent mottle types of virus X. Positive identification of potato viruses can be made only when certain characteristics of the virus such as temperature relations, physical properties, differential host range, cross protection reaction, local lesion reaction, transmission, insect vector-virus relations, reaction of potato varieties, and existence of strains are known. An attempt to determine these characteristics in potato virus A was made. A preliminary report has been presented (11).

A wild species of the Solanaceae, *Nicandra physaloides* (L.) Gaertn., was used as a systemic indicator host and for strain evaluation of Virus A. Two varieties of *Solanum demissum* Lindl. (4, 8) were used extensively as local-lesion hosts. *Lycium halimifolium* Mill., *L. rhombifolium* (Moench) Dippel, and *L. barbarum* L. also reacted to mechanical inoculation with virus A by production of chlorotic local lesions. Mechanical inoculation to *Lycopersicon pimpinellifolium* (Jusl) Mill. induced systemic necrosis. The two varieties of *S. demissum* and the 3 *Lycium* species also produced a type of local lesion when inoculated with at least one of the 10 strains of virus Y (5) and 7 strains of virus X (10) secured from desiccated stock cultures maintained at the Madison laboratory. *L. pimpinellifolium* failed to produce systemic necrosis within 7 days of inoculation with the above listed virus X or virus Y strains.

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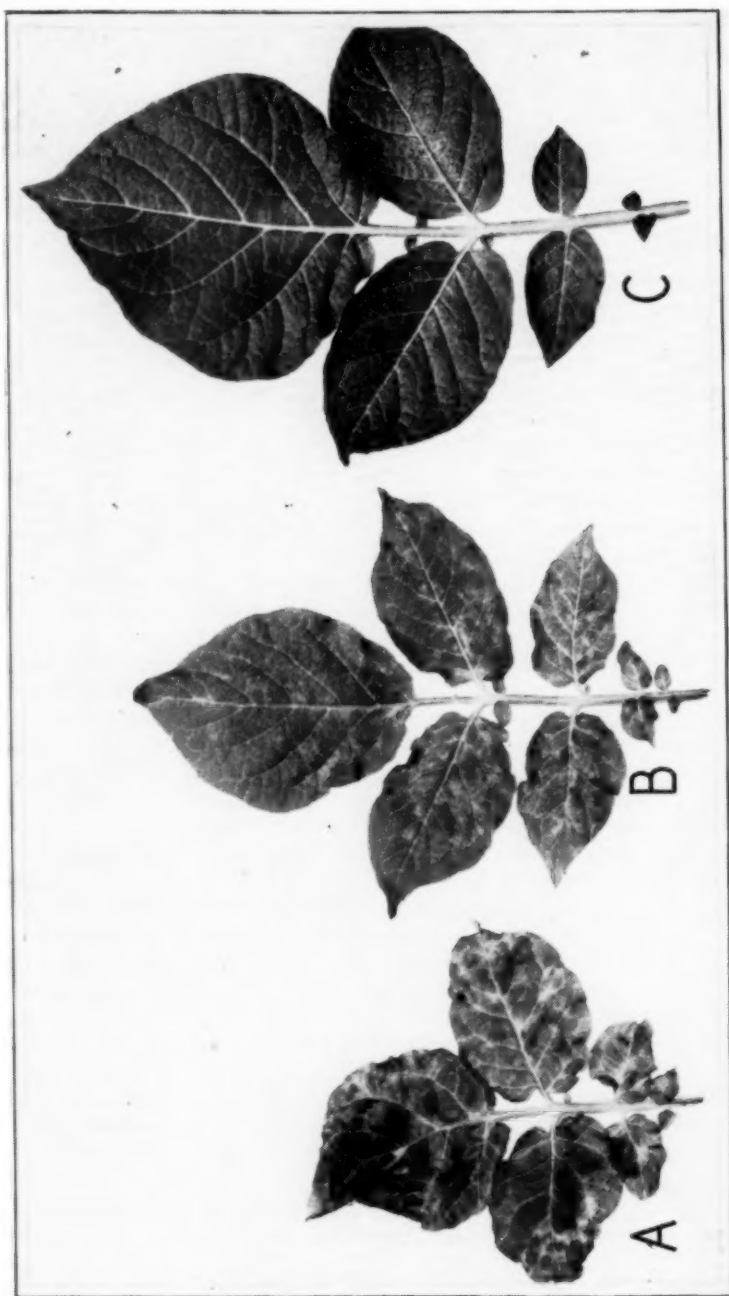


FIGURE 1.—Systemic symptoms at 18° C. on Green Mountain potato infected with virus A. A, Crinkle mosaic type. B, Mild mosaic type. C, Uninoculated control.

Plants from 132 single tubers of Green Mountain and Triumph potatoes infected with virus A from major potato growing areas of the United States and Canada were evaluated. *N. physaloides* was selected as a differential test host because of the wide differences in its reaction when infected with strains of virus A. The peach aphid, *Myzus persicae* (Sulz.) was used in all transmissions. Three distinct symptom types (mild, moderate and severe) were separated from the 132 tuber isolates. The severe type (group 3) was most prevalent in the Triumph isolates. Group 1 was characterized by vein clearing and slight stunting; group 2 by vein clearing, stunting, and diffuse mottle; and group 3 by severe necrosis, leaf crinkling and stunting as indicated in figure 2. By the spot necrosis reaction (5, 7, 10) on tobacco (*Nicotiana tabacum* L. var. Havana 38) the test hosts showing symptoms of virus A infection were checked systematically for virus X and virus Y contamination.

Cross-protection tests showed that *N. physaloides* infected with the mild strain of virus A was not susceptible to further infection with the more virulent strains, indicating that the 3 groups consisted of distinct strains of the same virus.

The strains of virus A had distinct differences in physical properties. Strains 1 and 2 were inactivated at dilutions of more than 1:10 and strain 3 was non-infectious at 1:50. Strain 1 was inactivated after aging *in vitro* for 12 hours and strains 2 and 3 remained infectious for 12 hours but were non-infective after 18 hours. In thermal inactivation tests, strain 1 was non-infective after heating to 44° C, whereas strains 2 and 3 were inactivated at 52° C.

The virus concentration in *N. physaloides* plants infected with each of the three virus strains was determined by mechanical inoculation to excised leaves of *S. demissum*. No consistent difference in concentration was detected between strains. Symptom differences were not due to virus concentration.

The reaction caused by the three virus A strains on Green Mountain plants infected with mild, moderate, and severe mottle types of virus X, respectively, showed that a complex of the severe strain of virus A and the severe mottle type of X incited a milder disease than did the combination of either the mild or the moderate strain and the severe X. Mosaic symptoms on potato varied considerably depending on the strains of both virus X and virus A, but a severe strain of virus A did not always incite the most severe mosaic symptoms.

When the potato varieties Irish Cobbler (12, 17), British Queen, and Up-to-Date (3) were grafted with scions from a single virus-A-infected plant of seedling 41956, the resulting top necrosis varied from mild to severe as noted in figure 3. In some instances, no top necrosis was observed. Tubers from these graft-inoculated plants usually exhibited external and internal necrosis. Top necrosis was not evident in grafted plants of the Kennebec variety, and the virus was not recovered. Severe tuber necrosis was correlated with severe top necrosis in field-immune varieties.

Cockerham (4) indicated that the lethal necrotic reaction, designated as field immunity or top-necrosis, upon which intolerance to virus A depends, is inherited as a dominant character. Irish Cobbler is top-necrotic to virus A and thus is field immune (12, 17). This form of immunity

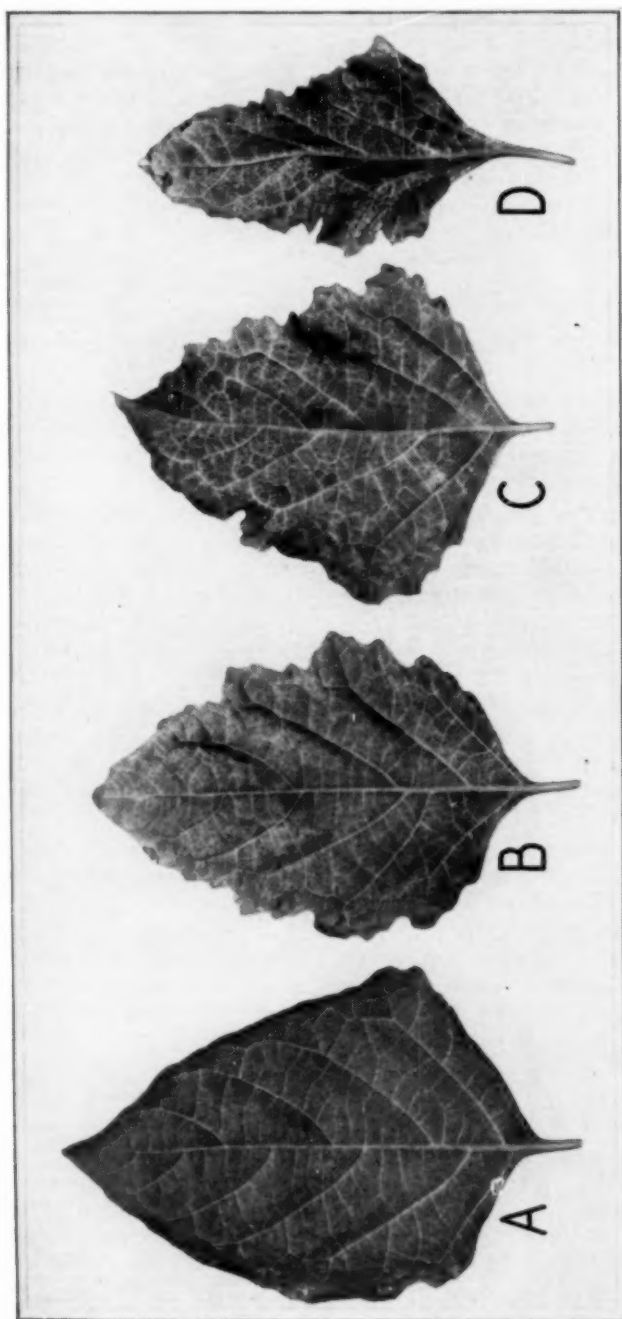


FIGURE 2—Leaves of *Nicandra physaloides* from plants at 24° C., mechanically inoculated with virus A. A, Uninoculated control. B, Strain 1. C, Strain 2. D, Strain 3.



FIGURE 3.—Irish Cobbler at 18° C., 30 days after grafting with a scion from a virus-A-infected plant of seedling 41956, showing top necrosis, leaf drop, and slight superficial necrotic streaking of the stem.

or intolerance is carried over in many seedlings from crosses in which varieties of this type are used as parents. Kennebec, related to Irish Cobbler, Katahdin and Chippewa, is field-resistant to virus A, but not top-necrotic.

The peach aphid, *M. persicae*, was found to be an efficient vector for virus A. Host-vector relationships showed that virus A was of the non-persistent type. With a pre-infection feeding starvation period of one hour, the acquisition threshold was 15 seconds. Viruliferous aphids were able to transmit the virus to healthy plants in a feeding period of 15 seconds; with feeding periods of 5 and 10 minutes, they infected two consecutive plants. After a post-infection feeding starvation period of 30 minutes, the aphids became non-viruliferous.

Although a synergistic reaction occurred between virus A and strains of virus X in Green Mountain and Triumph potatoes, a similar reaction was not demonstrated on tobacco. Combinations of virus A with a strain of cucumber mosaic virus (9), with Holmes' masked tobacco mosaic virus (6), with potato virus X^D(1), or with strain 12 of potato virus Y (5) on White Burley tobacco yielded only normal symptoms of the four test viruses.

(Abstracted from Wis. Agr. Exp. Sta. Res. Bull. 180, 1-37, 1953.)

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MAINTENANCE OF VIRUS X-FREE POTATOES¹JAMES MUNRO²

The relative importance of potato virus X has been much increased of recent years by the efficient control of potato virus Y and the leaf roll virus. According to Bawden *et al.* (5), virus X now probably causes more loss of the crop than the other two combined. Bald and Norris (4) also claim that the losses from potato virus X in Australia are as serious as the losses from all other viruses combined.

Although potato viruses Y and A may produce faint or barely distinguishable symptoms in certain varieties, it is generally the presence of potato virus X in potato stocks that creates doubt and uncertainty for the potato inspector and the experienced grower. Bald (1) suggests that those indefinite differences between plants within a crop are usually caused by a strain of virus X.

REDUCTION IN YIELD

It has been proven to the satisfaction of workers in several countries that mild strains of virus X can reduce the yield of potato crops. According to Bald (1) a loss in yield is inevitable when a plant becomes infected with a virus disease of the mosaic type, and in Australia he found that masked strains of virus X could reduce the yield of a crop by 12 per cent. Stapp (32) estimated the annual average reduction in yield in Germany from this source, as 10 per cent. In America, Schultz and Bonde (28) reported that from their experiments the loss in yield from virus X ranged from 9 to 22 per cent, and they recommended that varieties immune to virus X be developed. Smith and Markham (31) in England inoculated several varieties with a very mild strain, infection produced no leaf symptoms, but the yield of the inoculated plants was 12 per cent less than the controls.

Despite the evidence from many sources that mild strains of virus X significantly lower the yield of a potato crop, Clinch and McKay could not obtain that confirmation in their work (8,9).

They (8) carried out yield trials on the effect of mild strains of virus X, on two clones of the variety Up-to-Date. These results, on the whole, were indeterminate and they concluded that the reactions of different clones of the same variety to mild strains of virus X were variable.

The variety used by Clinch and McKay is a very late maturing one and the plants of most varieties that die down from early September onwards, in Ireland and in the British Isles, do so prematurely from the effects of *Phytophthora infestans* (Mont.) de Bary. Scott (36) found that the presence of a virus in a potato plant induced early ripening, and Bald

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Although potato viruses Y and A may produce faint or barely distinguishable symptoms in certain varieties, it is generally the presence of potato virus X in potato stocks that creates doubt and uncertainty for the potato inspector and the experienced grower. Bald (1) suggests that those indefinite differences between plants within a crop are usually caused by a strain of virus X.

REDUCTION IN YIELD

It has been proven to the satisfaction of workers in several countries that mild strains of virus X can reduce the yield of potato crops. According to Bald (1) a loss in yield is inevitable when a plant becomes infected with a virus disease of the mosaic type, and in Australia he found that masked strains of virus X could reduce the yield of a crop by 12 per cent. Stapp (32) estimated the annual average reduction in yield in Germany from this source, as 10 per cent. In America, Schultz and Bonde (28) reported that from their experiments the loss in yield from virus X ranged from 9 to 22 per cent, and they recommended that varieties immune to virus X be developed. Smith and Markham (31) in England inoculated several varieties with a very mild strain, infection produced no leaf symptoms, but the yield of the inoculated plants was 12 per cent less than the controls.

Despite the evidence from many sources that mild strains of virus X significantly lower the yield of a potato crop, Clinch and McKay could not obtain that confirmation in their work (8,9).

They (8) carried out yield trials on the effect of mild strains of virus X, on two clones of the variety Up-to-Date. These results, on the whole, were indeterminate and they concluded that the reactions of different clones of the same variety to mild strains of virus X were variable.

The variety used by Clinch and McKay is a very late maturing one and the plants of most varieties that die down from early September onwards, in Ireland and in the British Isles, do so prematurely from the effects of *Phytophthora infestans* (Mont.) de Bary. Scott (36) found that the presence of a virus in a potato plant induced early ripening, and Bald

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(3) observed that when immature virus X-infected plants and virus X-free plants were harvested at the same time, there was no difference in yield. When, however, they were harvested after they had died down naturally, the X-free plants yielded significantly higher than the X-infected plants. When a crop with simple mosaic and a healthy contiguous crop of the same variety are infected simultaneously and then destroyed with late blight, the bulking of tubers within the virus infected crop is further advanced towards the ultimate yield than is the healthy crop. Muller and Munro (21) also found that the retarded fructification of late blight spores on virus infected foliage was such that an epidemic would move faster through a virus-free crop than through a virus-infected crop of the same variety growing under similar conditions. This quicker kill of the foliage, and the slower bulking of tubers in the virus-free plants would tend to cancel out any increased weight of crop over one with a slight or mild disease caused by a virus infection.

STRAINS OF POTATO VIRUS X

Careful roguing of seed potato crops over the past three decades seems to have eradicated most of the naturally occurring strains of potato virus X that cause severe diseases. The recent work on the effect of virus X on yield has been carried out largely with strains that caused a mild or no apparent disease on the varieties used. However, there is evidence that severe strains still occur naturally in the field. Ladeburg *et al.* (16) found and MacLeod (17) reported several virulent strains occurring naturally and commonly in potato crops. Clinch of Ireland (7) and several of her colleagues found a strain of X in several parts of the country that produced symptoms on certain varieties of potatoes typical of those caused by a severe strain of potato virus Y. This may be partially explained in that the effect of one strain upon a variety is not necessarily an indication of its effect on all varieties. Roberts *et al.* (27) could find no evidence that masked strains underwent rapid conversion into severe strains. Hutton (13) thought that separation of strains by potato seedlings may explain the origin of masked strains commonly found in potato varieties. It may also provide an explanation for the occurrence of apparently new virulent strains in relatively new varieties of potatoes which are susceptible to virus X (15). Hutton and Peak (14), suggest that in evolution it is possible that avirulent strains preceded virulent strains, and that avirulent strains could remain undetected in certain hosts until transferred to a host in which it reacts as a severe strain. But even in the same variety certified as free from visible virus diseases in one year, it is commonplace to find an appreciable number of plants showing simple mosaic in the following year. This is interpreted (5) as the result of the segregation of a strain more virulent to that variety from the mild one dominating the stock. On the whole, constant roguing has tended to eliminate those strains that cause obvious leaf symptoms in most of the popular varieties, but the symptoms induced in a potato variety or a seedling by any one strain should not be expected to follow the same general trend in all varieties.

THE NEED FOR VIRUS-FREE POTATO STOCKS

That there is a need for X-free potatoes in many countries is evident by the sustained popularity of certain old varieties, and the constant demand for them in the higher seed grades. New varieties are being introduced yearly with justified claims to disease resistance coupled with good quality and heavy cropping propensities, yet the older varieties like King Edward and Majestic in Great Britain, Up-to-Date in Australia and Green Mountain in America still retain their old popularity despite the difficulties of finding these varieties, even in small quantities, in a virus-free state. Many years ago Salaman exclaimed that he didn't really know what made a variety popular in the eyes of a grower, as many of the traits of the most popular varieties seemed so much at variance with the accepted qualities desired. Up-to-Date and King Edward in Britain are the two varieties more susceptible to blight than any other varieties grown there. Majestic, the most popular variety among growers in that country seems to have little or no resistance to any of the common potato viruses, yet there have been more demands for virus-free Majestic than for all other varieties put together.

The often suggested plan to infect a stock with a mild strain to prevent further infection is not a substitute for virus-free stocks. It has been assumed that potatoes infected with a mild type of virus X are protected against infection with a severe strain, but investigations by Ladeburg *et al* (16) have clearly demonstrated that this is not always the case, and work by Matthews (19) indicated that he also had found like results. Obvious single stem infections of mild or severe strains on otherwise healthy looking plants occur perhaps more frequently than is appreciated. It seems that until we are able to produce varieties that are field-immune (hypersensitive) or immune from virus X, and which are also acceptable to the growers, there will be a need to maintain or to raise virus-free stocks of potatoes.

Perhaps even more important than the maintenance of old varieties in a virus-free state is the need to raise and maintain promising potato seedlings free from virus infection. Seedlings that are raised as late blight resisters and with other highly desirable qualities are too valuable to risk exposure to infection with virus X in the early stages of their multiplication. No matter how desirable in most respects, a new variety should not be released in a condition that reveals any of its weaknesses, however slight they are. It is difficult to observe a newly introduced and boosted variety with an unbiased eye. Claims of many desirable features within a variety are often taken to mean an absence of all weaknesses, and it is possible to multiply a seedling up to the stage of release in a virus-free state if care is taken. Seedlings may be raised and multiplied in a virus-free condition without difficulty if infected breeding material is kept in isolation or off the station altogether. Roberts (26) reported that of the many thousands of plants that have been raised in isolation plots as virus-free since 1946, in only one case has virus-X been found. Old varieties that are used as controls or late blight infectors should be either virus-free or field-immune to virus X.

VARIATIONS

Ladeburg *et al.* (16) thought that the chief disadvantage of such an undertaking as raising virus-free stocks would be the difficulty of preventing infection during the period of increase and the constant renewal of virus-free stocks for commercial seed growers; whereas the real difficulty lies largely in the replenishment of new selections of virus-free material from commercial stocks to replace the virus-free stocks that are changing from desirable to less desirable types. Experience has shown that it is much more difficult to obtain and maintain a desirable type of a variety free from variations within that variety than it is to keep it virus-free. Dr. Salaman's nucleus stocks of virus-free varieties, now in the care of the National Institute of Agricultural Botany, Cambridge, were collected during the nineteen-thirties. Replacements of certain stocks within this collection began in 1948 shortly after it was taken over from the Plant Virus Research Station at Cambridge. At this time there were three distinct clones of the variety Majestic in the collection that had been multiplied continuously under glass for many years. These clones were wholly free from virus but when grown under conditions of good potato culture, not only were there obvious foliage differences between clones, but there were also marked differences in cropping capacities in favor of a good commercial type that had been recently introduced. Their foliage differences were largely an appearance of lowered vigor with reduced size and slight distortion of the leaflets.

When Bald (2) made his virus-free selections of Up-to-Date he had thirteen clones. Of these thirteen clones one was discarded because of bolter characteristics, and there were definite agronomic differences amongst the other twelve. Roberts (25) made selections only from the most desirable types of his chosen varieties when he started his virus-free propagation scheme in Perthshire, Scotland.

Scott's work (36) with a feathery variation of the variety Kerr's Pink showed that this healthy variation gave a yield in total weight of 21.5 per cent less than the normal commercial type, but 84 per cent less in weight of tubers that would not pass through a two-inch square mesh. The variety Kerr's Pink was introduced in 1917 and about twenty years later there were at least twenty known variations from the desirable type of that variety. Scott also reported (36) that wildings and other variations may reduce a yield from 50-95 per cent of salable produce.

The investigations that have been made to determine the frequency with which variants arise in pure stocks have shown that in Arran Pilot, one of Britain's most popular early varieties, about three in every thousand normal plants annually assume the semi-bolter condition under the environmental conditions existing around Edinburgh (10). Semi-bolter variations are taller and later in maturity than the normal plants of a variety, and they are most commonly found in early maturing varieties.

Freedom from virus in a variety (25) is doing much to evaluate clonal variations, and in this evaluation the choice of desirable types as laid down by an authority such as the Scottish Department of Agriculture for Scotland, is being confirmed.

MAINTAINING STOCKS VIRUS-FREE

Great Britain. The National Institute of Agricultural Botany, Cambridge, is one of the official bodies that operate a virus-free potato scheme in Great Britain. Selections are made in the best seed growing areas and they are multiplied initially in a greenhouse at Cambridge.

Further stages of multiplication are made in cool humid wind-swept areas of Northern Ireland with a final multiplication, before commercial distribution, in the stock seed areas of Scotland. The production of virus-free potatoes is not vested in any one body. Recognized stock seed growers in Scotland who are in suitable areas for such work, and who have the required facilities for virus testing, may apply for virus-tested certification of their stocks. There are several such growers regularly producing virus-free stocks for commercial distribution. Although such potato stocks are officially named Virus-Tested, it is not certified as of this grade if any virus is revealed to be in the stock by the official check tests that are made by the serological and plant indicator methods.

As most of the virus-free material in Great Britain is raised from single-plant selections, virus tests by the growers are made by the plant indicator method because of its simplicity. In the early stages of multiplication all plants are tested once or twice each year. In the later stages up to and including the final stage immediately before commercial distribution, only random tests are carried out.

The only official certification scheme for virus-free stocks in Great Britain is conducted by the Department of Agriculture for Scotland (11). The scheme was initiated in 1950 with four growers and a total of thirty-one acres. This year there are seven growers and an expected acreage in excess of seventy. According to MacIntosh (18) the scheme is successful and only an occasional crop has been failed through virus X. Leaf-roll was a major trouble in the early years when roguing was not allowed, but roguing-out of up to ten plants per acre is now permitted.

Crops grown from Virus-Tested stocks up to 1952 have been marked with a star in the Potato Stock Seed Register. Until the introduction of Virus-Tested Stocks, Stock Seed was the highest grade of seed available in Great Britain. However as these starred Stock Seed Crops have been found to be so much superior to the common run of the Stock Seed grade, a new and higher grade called Foundation Seed, has been introduced this year (18). Only stocks grown from Virus-Tested seed and Starred Stock Seed of 1952 are eligible for certification in the new grade. The maximum permitted tolerance of virus disease in this grade is two plants per acre of leaf roll and ten plants per acre of mosaic due to potato mosaic viruses.

Among both farmers and merchants there is a growing appreciation of the commercial value of virus-free stocks which is being reflected in the increasing demands for the popular varieties in this condition.

West Germany. The private potato breeding farms of Luneberger, Heide, make greater use of virus-testing and virus-free multiplication methods than any other area in West Germany. Their seedlings on trial and under multiplication in the field are maintained virus-free by serological tests for virus X, and by *Solanum demissum* L. indicator plant tests for virus A. Leaf-roll virus and virus Y infections which are said to be rare or slight in this province, are controlled by visual roguing.

Each farm has its own staff of technicians and a well equipped laboratory. Tests for virus X are made by the Stapp serological method that requires the use of a centrifuge, an incubator and a microscope. Petri dishes are used in the detached leaf method with *Solanum demissum* for virus A tests.

Stapp *et al.* (33, 34, 35) developed an efficient mass serological method of testing for virus X in potatoes that could be carried out by simply-trained technicians on these plant breeding farms. They adapted the serological precipitin drop test method initiated by Dounin and Popova (12) and the sera drying method of Mez (34) to produce paper wafers impregnated with virus X antiserum (35). These wafers, four millimetres square, are cut from sheets of thin white paper on which virus X-immune rabbit antiserum has been spread on both sides at the rate of about one millilitre per sixty square centimeters and dried over calcium chloride in a desiccator at room temperature. For controls, normal rabbit serum is treated in the same way. To make a test, a wafer of antiserum is placed at one end of a microscope slide and a wafer of normal serum at the other end; to each is added a drop of physiological saline solution and a drop of clarified sap of the plant to be tested. The slide is incubated at 23° C for 20 minutes and then examined under a microscope in a dark field at a magnification of 50X.

Holland. In Holland some half-million serological tests are carried out each year for the elimination of virus X from the Foundation stocks of the Dutch varieties (30). Potato virus X antiserum is produced in horses at the Laboratory for Flowerbulb-Research, Lisse, Holland, under the direction of Prof. van Slogteren. The supervision and administration of these tests, which are carried out for stock-seed growers, is under the control of the Netherlands Inspection Service (N.A.K.) (37). Holland is divided into thirteen provinces and at a centre or a joint centre for each province, a well equipped laboratory has been established by (N.A.K.). The virus X antiserum is distributed from Lisse to each of these laboratories where the trained staff receive and test hundreds of samples daily during the growing season (20).

The method of testing used in Holland is also by that of micro-serology. The details of procedure are similar to those of Stapp except that drops of antiserum and normal serum are used and not impregnated paper wafers, and the expressed potato sap is not centrifuged.

Union of South Africa. Virus X-free seed potato production in South Africa is centered at Riet River Settlement, an area protected by legislation for the production of virus-tested stocks (24). The area is isolated and disease-carrying aphids are rare in its hot dry climate. To maintain adequate isolation, regulations made under the Act are used to prohibit the entry of all unauthorized potatoes. The prohibited area includes the Settlement and all land within 10 miles of it, and this in turn is surrounded by dry grazing country.

Since the inception of the scheme until the present time, virus testing of stocks has been carried out at Pretoria. Facilities for virus testing on the spot are now being arranged at Riet River. These tests will be made on the foliage, instead of the tubers as is practiced at Pretoria (23). The State still maintains a nucleus of virus-free stocks for the renewal and replacement needs of the growers in the settlement.

Canada. The primary work of this type is to maintain our seedlings and nucleus sources of the two varieties, Canso and Keswick, virus-free, and to this end a mass serological slide drop-test method initiated by Bradley in 1951 (6) was introduced in 1952. It is fairly efficient without being costly.

The drop slide methods of Van Slogteren of Holland and Stapp of Germany require a certain minimum of equipment, consequently in each case the simplicity of the tests, and the number that can be carried out in any given time, is much reduced. The tests can therefore only be made in a laboratory.

The tests at Fredericton are made simply by squeezing a drop of sap from a potato leaflet on each end of a microscopic slide. To one drop is added a drop of suitably diluted virus X rabbit antiserum and to the other a drop of diluted normal rabbit serum. The drops on each slide are stirred with opposite ends of a wooden toothpick which is then discarded. Because infected sap causes a precipitation in the antiserum drop within ten seconds of stirring, the stirred drops can be examined almost immediately. The precipitation can be easily and clearly seen without the aid of a microscope, simply by holding it to the junction of a white light fluorescent tube and the edge of attached black paper or board. However the greatest advantage of this method of testing is that it can be carried out with equal efficiency in the field. During the summer months our tests are conducted on the headlands of potato fields with the aid of a small specially constructed hand-wagon or in the potato crop itself with a smaller easily maneuvered aluminum hand-wagon as shown in figure 1. This latter wagon can be folded up into a bulk of 41 x 28 x 5 inches for easy conveyance by automobile to different parts of the province.

EFFICIENCY OF METHODS OF TESTING

The Stapp and Bercks (35) and the van Slogteren (29) serological methods are very easy and effective ways for plant breeders and stock seed growers to test and rogue for potato virus X on the same day. They only require simple equipment and the developed technique is one in which technicians can be easily trained. The prime disadvantages are that they are not field tests and the number of tests that can be carried out in a day is much less when centrifuging, incubating and microscopic readings are necessary. However the gain to the plant breeder of the paper wafer test is still immense because it is the only way that he can effectively test large numbers of his seedlings and varieties. The incentive to plant breeders in West Germany to raise their own varieties in a virus-free state is much increased by the law that permits only the plant breeder in that country to be eligible for the highest official seed potato grade for his own varieties.

There may be no claims by van Slogteren and Stapp to absolute accuracy with their methods, but they do maintain that it is close to 100 per cent. The method used at Fredericton is not so efficient as those used in continental Europe, but the ease and speed with which large numbers of tests can be completed must far exceed any other known method. About one hundred tests can be made in thirty minutes by four technicians, either in the laboratory or in the field, exclusive of the time required

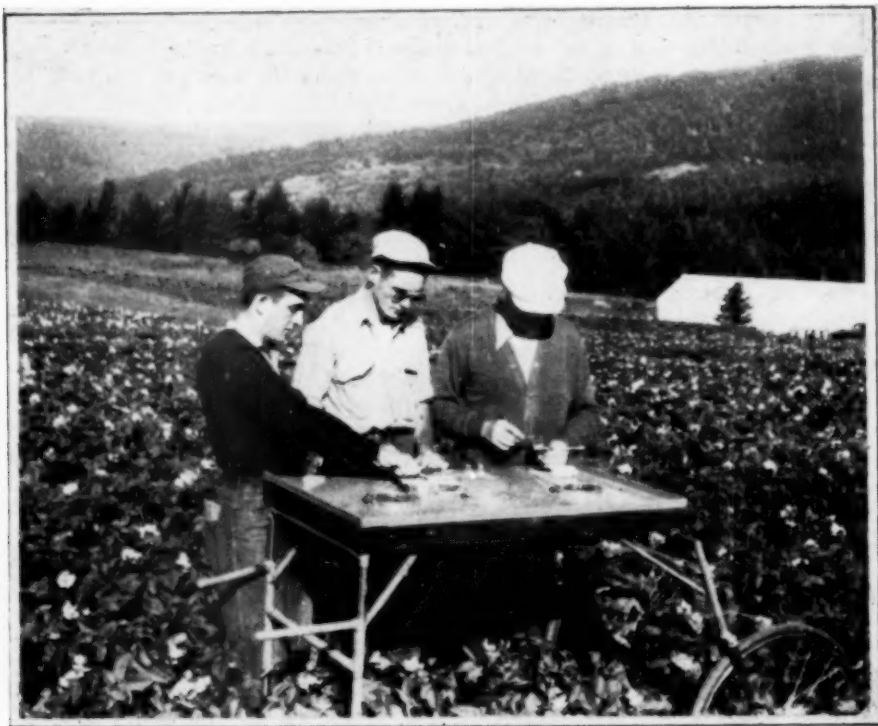


FIGURE 1.—Testing for potato virus X in the field. Note aluminum wagon with equipment which can be converted into small bulk for transport.

to collect the samples. Four men can do about 800 tests a day continuously over long periods, including the collecting of samples and allowing for fatigue. A car mirror is used as a source of light to observe the slides in our outdoor tests.

On the whole we find that this method of testing is about as efficient as tuber testing on to plant indicators. With each lot of antiserum from a rabbit we make serial dilutions with physiological salt solution, and each dilution is tested with freshly extracted crude sap from upper leaves of virus X-infected Green Mountain potato plants. The dilution that causes a precipitin reaction almost immediately is the one chosen for our test work. Dilutions of X antiserum for use in the field and in the laboratory are usually made up twice a day and on each occasion a check test is made with young leaves of a known infected plant.

In our experience with the simple field drop test method for the detection of potato virus X, check tests with *Datura stramonium* L. have always confirmed the positive slide results; but we do on occasion get up to 20 per cent of the infected plants giving negative results on the slides. This was found to be due, in part, to the slow formation of the precipitate and the consequent discard of the slide before it appeared. Despite the

precaution of delayed readings of series of slides, there seems to be occasional laggard reactors within most of the varieties and seedlings that we have tested so far. Similar experiences may have guided both Stapp and van Slogteren to make the refinements in their methods that are lacking in ours. Eventually our comparatively crude method may have to be improved before virus X can be wholly eliminated from our stocks. The method that we employ may only be of real value when a stock is infected with a high percentage of the virus, but much less so when only occasional infected plants remain in the stocks.

In the production of seed potatoes the most certain way of avoiding loss is to avoid virus infection (1), and it is only when healthy potato plants are grown in proximity to virus X-infected plants that there is any likelihood of a breakdown in virus-free stocks. To quote van der Plank (22) freedom from virus X is an elementary requirement for good seed, and seed free from virus X should be available as the ordinary article.

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POTATO PRODUCTION IN FLORIDA AS INFLUENCED BY
SOIL ACIDITY AND NITROGEN SOURCES¹

G. M. VOLK AND NATHAN GAMMON, JR.

The maintenance of strong soil acidity has been recognized generally in the past as a control measure for scab of Irish potatoes. The introduction of certain new commercial varieties which show resistance to the disease reduces this limitation to some extent (2). This is of particular interest because most plant species are known to grow best at a soil acidity more moderate than that found necessary for the control of scab. Apparently this may be true also for potatoes.

Recent investigations in Florida have shown a real need for general re-evaluation of soil pH and its effect on nitrogen supply (8). Investigators from other areas also have indicated that high soil acidity may be undesirable (3, 5). The reasons given are varied, probably justifiably so because of the differences between soils being considered. The conditions encountered in Florida may be peculiar to this state, but the responses to reduction of soil acidity have been so outstanding that a careful evaluation of the problem for other areas is indicated if such has not already been done.

Attention was first focused on the problem in Florida by the appearance of an unidentified type of leaf roll of potatoes.* It was the most severe on the very sandy soils and on relatively new lands. Analysis of soil samples showed the trouble to be associated with strong soil acidity and a high content of ammonia. The main plant symptom was a rolling upward and inward of leaf edges parallel to the midrib, as shown in figure 1. It could occur at any time in the life of the plant, but usually became most apparent about blossom time. Potatoes so affected matured earlier than normal and produced a low yield. A more detailed description of the disease is given elsewhere (8).

Prior to recognition of this trouble it had been shown conclusively that certain acid virgin Florida soils were abnormally limited in their ability to convert ammonia nitrogen to nitrate nitrogen, and that in some cases nitrification was still slow even after liming to raise the pH as noted in table 1. Samples of soil collected from areas where the leaf roll was present were similar, in that they were very acid and nitrification tests, which are tabulated in table 2., showed that conversion of ammonia to nitrate was very slow. Abnormally high amounts of ammonia were present for that time in the growing season. The addition of lime to raise the pH markedly improved the condition on old land, but had little or no effect on new land. The trouble was attributed at this time to the excess of ammonia nitrogen (6), but subsequent investigations showed this to be only part of the answer.

*A. H. Eddins, Plant Pathologist in Charge, Potato Investigations Laboratory, who cooperated throughout the work, first brought this problem to attention and stated that the trouble was not caused by a fungus, bacterium, or virus. This condition should not be confused with the virus disease commonly known as leaf roll.

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FIGURE 1.—Typical nutritional leaf roll of Irish potatoes (Sebago variety).

A comprehensive set of field tests was laid out on relatively new land which had carried only two crops, and on old lands where leaf roll was severe, in an attempt to verify the above conclusions and to determine methods of correction. These tests included application of various amounts and ratios of lime, nitrate nitrogen and ammonia nitrogen. Chlorine was held constant or omitted from comparative treatments, therefore was not considered to be a factor. From these tests came one very significant finding the first year. Leaf roll was severe where the amount of nitrate nitrogen available to the plant was low; but it did not develop where nitrate was high, regardless of ammonia level. The amount of nitrate found in the plant tissue correlated in similar manner, but there was no correlation with several other elements for which analyses were made as shown in table 3. However, it is possible that a high level of ammonia could enhance the disease by producing a larger, more susceptible plant. Leaf roll apparently could develop at any stage of growth of the plant at a time when the supply of nitrate nitrogen was deficient.

The results of the fertilizer trials are summarized in tables 4, 5, and 6. Table 4 contains data obtained on St. Johns fine sand in its third crop year. Leaf roll had been severe on the south end of the field the previous year, but none was present in the north end. There was a significant yield response to nitrate nitrogen where leaf roll was severe, but the greatest yield resulted where the soil pH was more favorable and no leaf roll developed. Leaf roll was obvious with treatment 1 (South), but did not

TABLE 1.—*Nitrification in Leon and Bladen fine sands.*

	Treatment		After 28 Days Incubation	
	CaCO ₃ Lime PPM.	Urea Nitrogen PPM.	Ammonia Nitrogen PPM.	Nitrate Nitrogen PPM.
Virgin Leon Fine Sand, pH 4.4 (Inoculated)*	0	0	4.1	0
	0	50	45.2	0
	2000	50	44.2	2.7
	2000	50	10.1	54.4
Cultivated Leon Fine Sand, pH 7.1	0	0	3.6	14.6
	0	50	4.0	50.3
Virgin Bladen Fine Sand, pH 5.3 (Inoculated)*	0	0	15.1	0.6
	0	50	55.7	0.6
	2000	50	37.0	14.8
	2000	50	10.2	73.2
Cultivated Bladen Fine Sand, pH 5.7	0	0	3.6	15.6
	0	50	3.3	57.9

*Inoculated with 1 per cent of cultivated soil of the same type.

Unpublished data by Shui-Ho Shih, graduate assistant, and the senior author. 1948.

TABLE 2.—*Nitrification in Bladen and St. Johns fine sands where nutritional leaf roll was serious.* (6)*

(Samples taken about 60 days after fertilization and planting)

Soil	Nitrogen in Field Samples		After 28 Days Incubation	
	Ammonia Nitrogen PPM.	Nitrate Nitrogen PPM.	Ammonia Nitrogen PPM.	Nitrate Nitrogen PPM.
St. Johns fine sand. Second crop on new land. pH 4.8	212 Limed to pH 5.9***	3	239 135	12 79
St. Johns fine sand. Second crop on new land. pH 4.0**	19 Limed to pH 6.0	1	79 81	2 7
Bladen fine sand. Old land. pH 4.2	79 Limed to pH 6.2	13	59 3	21 85
Bladen fine sand. Old land. pH 4.3**	22 Limed to pH 6.6	14	56 0	42 99

* The soils have base exchange capacities of 5 to 6 m.e.

** 50 PPM. Urea nitrogen added for incubation test.

*** Same soil limed for incubation tests.

TABLE 3.—*Analysis of rolled and normal potato tops—Sebago variety.*
(Plants 50 to 60 days old)

Plot	Treatment 2500 Lbs. 5-6-6	Soil Analysis			Plant Analysis							Plant Condition
		pH	PPM. NO ₃ -N	PPM. H ₂ -N	Per cent of Dry Weight							
Potato Laboratory Tests												
					NO ₃ -N	H ₂ -N	Ca	Mg	K	P	Fe	Na
6	No NO ₃	5.17	23	85	.18	.07	.96	.62	4.2	.53	.020	.025
8	2.1% NO ₃	4.85	54	65	.16	.06	.98	.62	5.2	.50	.020	.045
9	No NO ₃	5.22	3	40	.02	.16	.90	.83	3.7	.51	.020	.063
17	No NO ₃	5.76	3	56	.01	.18	.80	.67	2.8	.43	.022	.088
23	2.1% NO ₃	4.58	2	18	.02	.06	1.02	.70	4.4	.48	.019	.045
Bimini Tests												
4	No NO ₃	4.57	10	122	.03	.026	.72	.51	6.6	.51	.025	.063
5	2.1% NO ₃	4.27	38	64	.53	.032	.72	.58	5.8	.56	.020	.037
7	No NO ₃	4.08	10	69	.05	.052	.61	.68	6.9	.68	.017	.037
10	2.1% NO ₃	4.22	45	87	.32	.012	.61	.58	5.8	.58	.020	.037

TABLE 4.—*Effect of soil pH on response of potatoes to nitrate nitrogen applied in 2500 pounds of fertilizer per acre.*

Treatment No.	Pounds Nitrate Nitrogen Applied	Yield in Bushels per Acre	
		Formula	Units Nitrate Nitrogen
1	0	5-6-6	0.00
2*	19	6-8-8	.75
3	50	5-6-6	2.00
3-S**	50	5-6-6	2.00

* Grower's formula.

** Split application, 1,600 lbs. in drill and 900 lbs. at 59 days.

TABLE 5.—*Effect of increasing percentage of nitrate nitrogen on yield of potatoes.*

Drill Treatment	Per cent Nitrate Nitrogen in Fertilizer	Without Side-Dressing	With 125 Pounds of 13-0-44 Nitrate of Potash Side-Dressing
2500 lbs.	0.48	335 bus.	339 bus.
of	1.43	345 bus.	366 bus.
5-6-6	1.92	355 bus.	383 bus.

TABLE 6.—*Effect of side-dressing on yield of potatoes on very light Leon fine sand.*

Treatment No.	Fertilization		Yield Bushels per Acre
	Pounds of 5-7-5 at Planting*	Pounds of Side-Dressing at 42 Days**	
1	2,500	270, 13-0-44 Nitrate of Potash	321
2	1,800	270, 13-0-44 Nitrate of Potash	305
3	1,800	700, 5-7-5	283
4	2,500	80, Nugreen (urea)	271
5	2,500	None	261
6	1,800	None	259

* 1.0 per cent nitrate nitrogen.

** 35 pounds of nitrogen applied in these side dressings.

occur on treatments at pH 4.9 or where two units of nitrate nitrogen were used.

Table 5 shows similar data from an old area of Leon-Bladen soils with an average pH of 4.75. Lime produced an average increase of 37 bushels. The average increase resulting from raising the nitrate nitrogen level in the fertilizer from 0.48 per cent to 1.92 per cent was 44 bushels when followed by side dressing.

Table 6 shows the increase obtained from side dressing very light Leon find sand previously limed to pH 5.3. No leaf roll was present. There was a significant increase of 60 bushels due to side dressing with nitrate of potash.

As a result of the foregoing tests it was concluded that nutritional leaf roll is caused primarily by a lack of sufficient nitrate nitrogen to balance an otherwise normal amount of ammonia nitrogen available to the plant. The balance could be accomplished either by adding more nitrate at planting or as side dressing; or by the more practical way of liming to increase natural production of nitrate from the ammonia added in the fertilizer.

The reason for lack of recognition of this need for nitrate nitrogen by potatoes in the past may have been that soils usually used for potato production in other parts of the country do have an acceptable rate of nitrification of ammonia. However, a rolling of the potato leaves in late season might be mistaken for drought or natural malnutrition, where in fact a greater yield would have been produced by extending the growing period by the opportune addition of nitrate, if its deficiency were the real limiting factor.

Hundertmark and Allison, working in the Hastings area, conducted tests 1936 to 1939 which showed average yields of approximately 148 bushels and no special benefit from replacing 15 per cent of the ammonia nitrogen in 2000 pounds of a 5-7-6 fertilizer with nitrate nitrogen (4). An examination of the annual yields showed that for years of relatively high yield the nitrate was superior. A marked increase in productivity took place with the introduction of the Sebago variety and improvement in disease control practices. Probably part of the need for the increased percentage of nitrate nitrogen is this generally higher yield for the area.

Deficiency of potash probably was an enhancing factor in certain of the tests in Florida. Although in most instances potash was held constant in supply, in certain cases, especially on the lighter soils, the addition of nitrate of potash side dressing produced a yield increase which may be attributable, at least partially, to the potash. Figure 2 shows a comparison between 2200 pounds of 6-8-8 fertilizer at planting, and the same plus 220 pounds of 15-0-14 nitrate of potash as a side dressing about blossom time. Leaf roll was eliminated and the date of maturity of the crop markedly extended by the side dressing.

A better understanding of the value of careful control of soil acidity and the selection of nitrogen sources can be obtained by examining the soil factors which will influence recommendations for different soils. Figure 3 shows the correlation of yield with approximate soil moisture holding capacity (moisture equivalent) in a fairly typical field containing the range of soils usually found in the Hastings section.



FIGURE 2.—Effect of 15-0-14 nitrate of potash side dressing on nutritional leaf roll of potatoes on light strongly acid soil.

Right: 2200 pounds of 6-8-8 containing 1.5 units of nitrate nitrogen at planting.

Left: Same at planting plus 220 pounds of nitrate of potash at blossom time.

Excess moisture entering a soil but not retained by it will leach out nitrate nitrogen or other soluble plant foods. As the soil becomes more acid, the fertilizer bases such as potash and ammonia are leached more readily, as shown in figure 4 (7). The very sandy soils of low base exchange capacity, represented by the 4 m.e./100g. example in figure 4, are very susceptible to the effect of high acidity. Soils of the Hastings area range between the 4 and 20 milliequivalent examples given, with a general average of approximately 6 milliequivalents.

It follows that the soil pH should be maintained as high as practical without unduly encouraging scab. This has been set at pH 5.5 for the area now planted to the Sebago variety. A general rule for average soils of the area is to apply 200 pounds of limestone, either high calcic or dolomite, for each 0.1 unit below pH 5.5. This should be based on pH values taken in the fall, because values taken in late spring just after the crop is removed are found to be about 0.4 pH unit lower and are more unreliable as a measure of lime need. About 200 to 300 pounds of limestone per year are needed to offset fertilizer acidity under present practices. The use of dolomite to make fertilizers physiologically neutral was considered at first as a possible answer to the problem, but work by Dunton *et al.* (1) has shown that this limestone is relatively ineffective on the acidity of the fertilizer with which it is incorporated but is only of general cumulative benefit over a period of years.

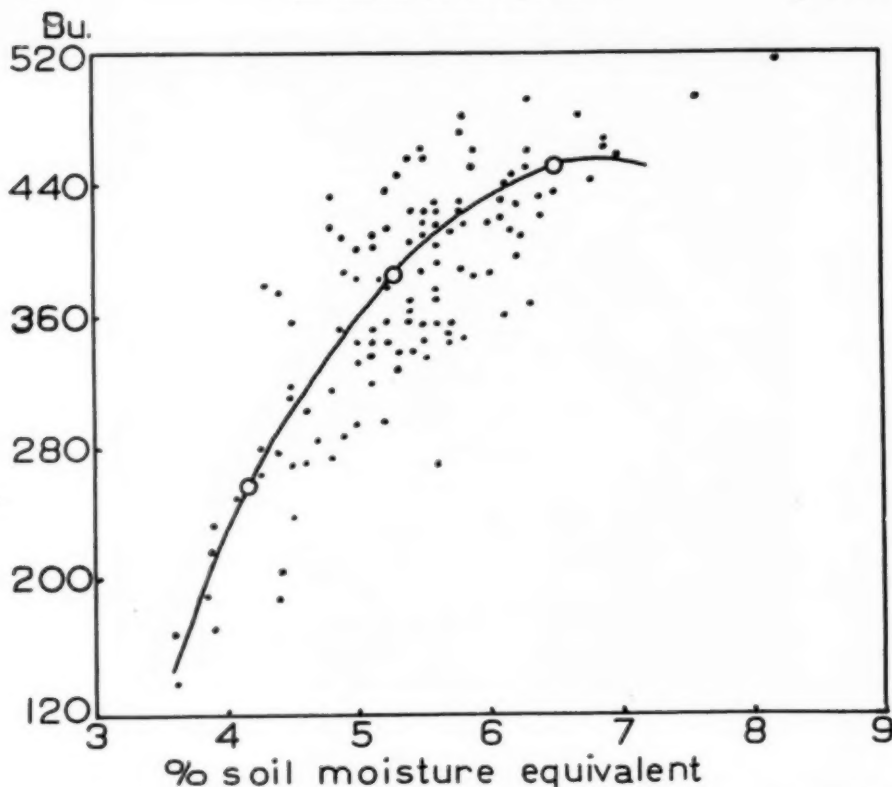


FIGURE 3.—Relation of yield of potatoes to soil type. Experimental points are indicated plot yields distributed over a total area of $2\frac{1}{2}$ acres. A moisture equivalent of 3 per cent indicates a very sandy soil, while 9 per cent approximates a loam soil. A range of 4 to 7 per cent in one field is common in the Hastings area. (The curve is drawn parabolic, $x = 7.17 - \sqrt{.0113(456-y)}$, to the three median points shown).

The recommendation for the percentage of nitrate nitrogen to be included in the fertilizer depends on whether or not new land is to be used and whether the soil acidity is so low as to require heavy liming. New lands not over three years under cultivation apparently have not established an efficient nitrifying microbiological population, nor have acid soils below approximately pH 4.8. In such cases, additional nitrate is needed in the drill and as side dressing, otherwise the general recommendation for the area is to supply one fifth of the nitrogen from nitrate sources.

The potential value of the new scab-resistant varieties of potatoes is obvious for the acid mineral soils of Florida. Acceptance of the Sebago variety for the Hastings area is fortunate in this respect. Its resistance to scab, combined with what has been suggested as a relatively low virulence of the scab organism for our particular season of production, has permitted the initiation of a program of liming that, along with the increase in nitrate nitrogen percentage in fertilizers, probably is partially responsible for the recent increase in productivity of the area. The liming program was started as a result of the work on nutritional leaf roll, with the result that this

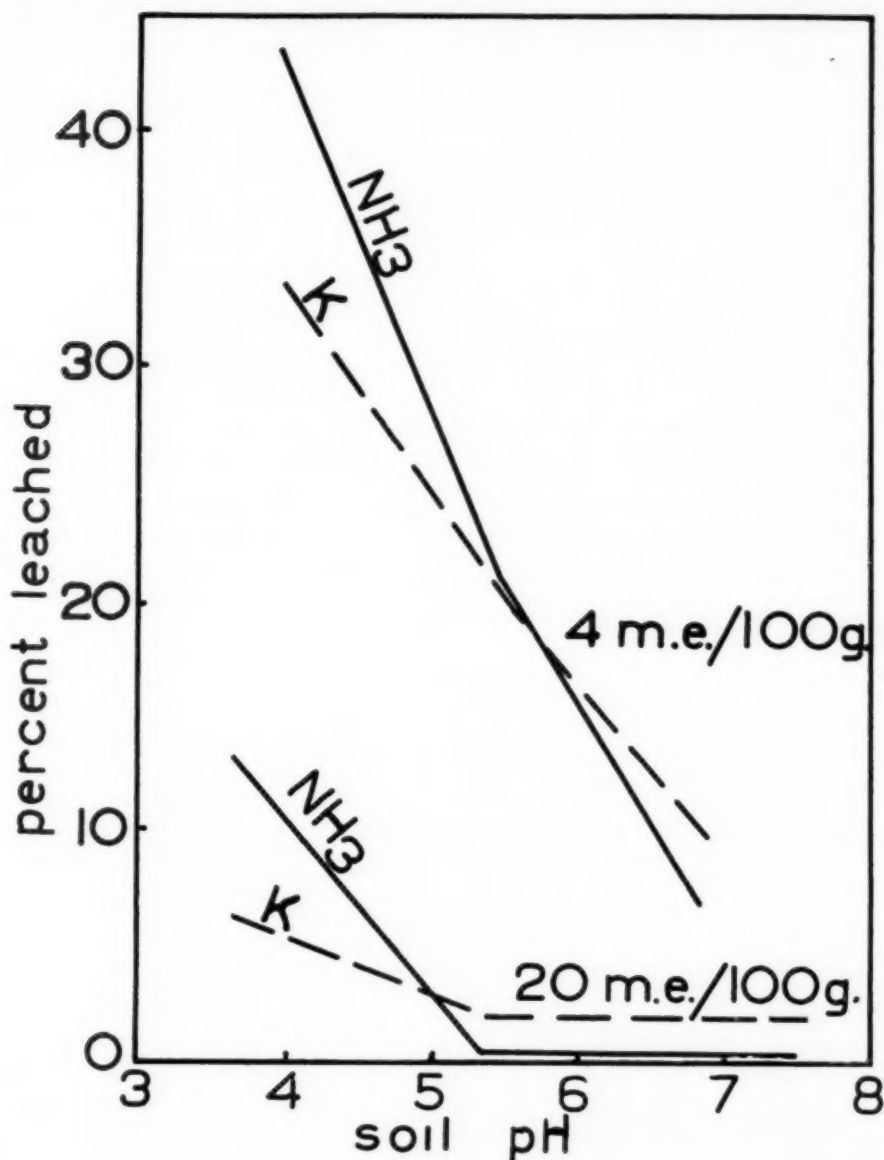


FIGURE 4.—Effect of soil pH on the retention of potassium and ammonia following application of 200 pounds of potash as the sulfate and 100 pounds of ammonia nitrogen as ammonium nitrate. This was applied to a 9-inch depth of soil and leached 36 hours to produce 2½ inches of leachate (7).

trouble is now practically non-existent in the area.

There is still much room for improvement in yield in the Hastings area consideration:

1. Increased use of side dressings, particularly on lighter soils and during years of heavy rainfall.
2. Improved water control, especially at the critical period determining tuber set.
3. Reduction of chlorine in the fertilizer, making possible increased rates of application of the major elements without increasing the hazard of toxicity.

The present rates of nitrogen and potash application for the area probably are not sufficient for yields of more than 400 bushels per acre. Many fields are capable of far exceeding this figure if proper water control is available, and should be fertilized more heavily if maximum production is to be realized.

The findings for the Hastings area will also apply to other acid flatwoods soils, notable at LaCrosse and in South Central Florida, which are being brought into production.

There is apparently no particular problem on the heavier mineral soils being used for potatoes in West Florida. Neither does it exist for the marls of the Homestead area nor the peat and muck soils under production. Natural production of nitrates on the marl and organic soils is so high as to be a possible problem in itself.

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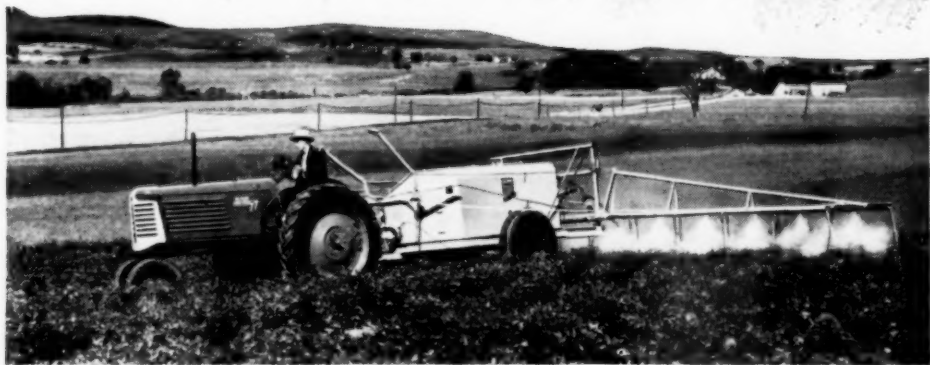
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